

25 years
of
botany

LICHENOLOGY IN NORTH AMERICA
1947-1972

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In assessing the advances of lichenology in North America during the past quarter century it is essential to have an understanding of the situation as it existed at the start. The literature was not very abundant, nor was it readily available to many people in understanding or in fact. The then recently published manual by Bruce Fink (1935) was highly technical and difficult to use. His excellent *Lichens of Minnesota* (1910) with more comprehensive descriptions was occasionally on the secondhand market. Some of us were able to purchase Tuckerman's *North American Lichens* (1881, 1888) and used these with some difficulty in understanding how terms should be applied to the lichens at hand. The very fine literature of Europe was unavailable to most would-be lichenologists because of its rarity in libraries as well as language barriers. The monographs on North American lichens were rare indeed—Willey (1890) on *Arthonia*, and Berry (1941) on *Parmelia*. The brightest spot was with respect to the genus *Cladonia*. The very great and penetrating works on this genus by Alexander Evans and his prompt and willing help to beginners plus the aid he enlisted of Raymond H. Torrey fostered an interest in these lichens, especially along the East Coast.

Other workers active in lichenology in this period included A. W. C. T. Herre, who had just returned from his long stay in the Philippines working on fishes and resumed work and publishing on lichens. His 1913 thesis on the lichens of the Santa Cruz Peninsula is still very valuable. Herre worked for a time at Stanford University before he was required to retire but continued to be helpful to many by correspondence. Carroll W. Dodge had published on the Antarctic lichens (Dodge & Baker, 1938) but also had several students, including E. C. Berry, George A. Llano, and E. D. Rudolph. Grace Howard at Wellesley College was working on the lichens of the state of Washington which she published (1950) after her retirement and in association with the University of Washington. At the University of Michigan Joyce Hedrick Jones continued as curator of the Bruce Fink collections which had been acquired by that university. Several students, including Henry A. Imshaug, were being guided by the University of Michigan mycologist, Alexander H. Smith. The New Jersey rhododendron grower Guy G. Nearing, who had been interested by Raymond Torrey in lichens, was

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in this period publishing his *Lichen Book* (1947), hand setting the pages with his own fonts and printing the parts on his own small hand press. We must include Margaret Fulford of the University of Cincinnati who stirred the interest of several students, including W. L. Culberson, in continuing work with lichens. W. L. Dix, another of Torrey's disciples and a Latin teacher in Staten Island schools, was also active as a student of *Cladonias*. Babette Brown Coleman was working on the ecology of lichens in upstate New York, and Josiah Lowe was producing an excellent paper on *Lecidea* in the Adirondacks. Roy Latham of Long Island, yet another of Torrey's coterie, was interested in *Cladonia alpestris* and *Cetraria islandica*. I. Mackenzie Lamb, later to become Director of the Farlow Herbarium, was still abroad and had not migrated to this continent. When all is considered, the active number of lichen students a quarter century ago was really rather small. The progress and interest in this group of organisms as objects of study has accelerated and deepened immensely. The breadth of approaches has also widened.

LICHEN CHEMISTRY

Probably the most significant advance in the study of lichens on this continent has been the application of chemistry to lichen taxonomy. Although founded upon earlier researches in Germany by Hess and Zopf, it was not possible to advance much until the work of Asahina in Japan, commencing in the 1930's and 1940's and continuing to the present, made it possible to identify lichen substances by the microscopic crystals formed by the reactions of organic reagents with extracts requiring but a tiny portion of a lichen thallus. This fascinating new development was enthusiastically embraced by Alexander Evans at Yale and led to a long series of studies on the genus *Cladonia*, which appeared in papers from 1943–1955 (list in Thomson, 1967c). At about the time the Culbersons were at Wisconsin as graduate students, they became interested in the field of lichen chemistry and taxonomy and have collaborated since with remarkable results. A long series of papers by either William or Chicita or both has culminated in the production of the 1969 book *Chemical and Botanical Guide to Lichen Products* by Chicita F. Culberson and its 1970 supplement in *The Bryologist*. These are landmark contributions to the field of lichenology. Chicita Culberson has also been developing to a fine art the use of thin-layer chromatography in the solution of problems involving lichen chemistry, and she and students working with her will be contributing much in that field which still has many, many opportunities to exploit. The 1970 paper on a standardized method for the identification of lichen products is an important contribution which is already influencing procedures in lichen research (C. F. Culberson & Kristinsson, 1970). Much lichen chemistry as applied to taxonomic problems has also been contributed by Mason E. Hale, Jr., starting with papers published from 1952 on. His discussion of the relationship between chemistry and the evolution of lichens (1966) has been influential in the development of thought in that field and will be recognized as such. Another earlier (1956) paper on the fluorescence of lichen products brought to this country the use of a new and helpful tool, the use of ultraviolet light, in lichen systematics. It provided one more set of char-

acteristics by which decisions in identification could be made. Of course, the fluorescence is dependent upon the products contained in the lichens, but this tool has been used to great advantage in the systematics of *Thamnolia*, *Pyxine*, *Cladonia*, and *Cetraria*, among others.

LICHEN TAXONOMY

The status of revisions of the genera of lichens of North America is very uneven. Few papers have been published on the crustose lichens: *Placynthium*, *Arctomia*, *Vestergrenopsis*, *Massalongia*, and *Koerberia* by Henssen (1963a-d, 1969), *Ochrolechia* by Howard (1970) and Versegny (1962), *Rhizocarpon* (Thomson, 1967a), *Cyphelium* (Weber, 1967), the Trypetheliaceae (Johnson, 1959), *Haematomma* (W. L. Culberson, 1963), and the Heppiaceae by Wetmore (1970). Rudolph is working upon *Caloplaca*, Sheard upon *Rinodina*, Imshaug upon *Buellia*, Hale upon Thelotremaceae, R. A. Anderson upon *Lecidea*, Dibben upon *Pertusaria*, and Thomson upon *Staurothele*, but many more genera need to be studied in the decades ahead. The larger foliose and fruticose lichens have been much better studied, and the past two decades especially have vastly improved our knowledge of these. There are larger papers now available on *Alectoria* (Motyka, 1964), *Anaptychia* (Kurokawa, 1962; W. L. Culberson, 1966), *Baeomyces* (Thomson, 1967b), *Cetraria* and related genera (W. L. Culberson & Culberson, 1965, 1967, 1968), *Cladonia* (Thomson, 1967c), *Parmelia* (Ahti, 1966, 1969; Hale, 1965; Hale & Kurokawa, 1964), *Peltigera* (Thomson, 1950), *Physcia* (Thomson, 1963), *Pseudevernia* (Hale, 1968), *Nephroma* (Wetmore, 1960), *Tholurna* (Otto, 1972), and Umbilicariaceae (Llano, 1950, 1956). I. M. Lamb continues with the preparation of his immense monograph on *Stereocaulon*. In addition to these are many shorter papers which can be found in the "Recent Literature on Lichens," listings regularly published by W. L. Culberson in *The Bryologist*. Of indispensable help to the lichenologist is I. M. Lamb's *Index Nominum Lichenum* (1963) which continued the Zahlbruckner *Catalogus Lichenum Universalis*.

FLORISTICS

The greatest activity apparent in North American lichenology has been a spate of papers inventorying the lichens of local areas or states. Many of these papers have been stimulated by the policy of the American Bryological and Lichenological Society holding its meetings with the A.I.B.S., and as the meetings were held in various parts of the continent from New England to Florida, California, Washington, or Alberta, the associated forays have been reported upon with concomitant increase in knowledge of the lichens of those areas. There are over a hundred papers produced during this period, too numerous to list here, but of interest may be the diversity of the states represented: Alabama, 3 papers; Alaska, 15 papers; Arizona, 4 papers; Arkansas, 1 paper; California, 5 papers; Connecticut, 3 papers plus a long series by Evans; Delaware, 1 paper; District of Columbia, 1 paper; Florida, 2 papers; Georgia, 1 paper; Idaho, 4 papers; Louisiana, 2 papers; Maryland, 1 paper; Michigan, 4 papers; Minnesota,

3 papers; Mississippi, 1 paper; Missouri, 1 paper; Montana, 2 papers; New Jersey, 1 paper; New Mexico, 3 papers; New York, 4 papers; Oklahoma, 2 papers; Ohio, 2 papers; Oregon, 1 paper; South Dakota, 1 paper; Tennessee, 3 papers; Utah, 1 paper; Virginia, 5 papers; Washington, 8 papers; Wisconsin, 6 papers; and Wyoming, 1 paper. In addition to records in these geographically oriented papers, other states have been represented by records in papers upon particular taxonomic groups. It is sufficient to call attention to the fact that many states are not represented on the above lists and are as yet to be worked upon. Even the 30 mentioned above are incompletely known and still will be needing much more work in the future. Our Canadian colleagues, I. M. Brodo, George Otto, C. D. Bird, J. W. Sheard, D. F. S. Richardson, Jan Looman, George Scotter, J. D. H. Lambert, Vladimir Krajina, and R. E. Longton are all busy adding to the regional information on their side of the border.

This period seems to have been a period of stock-taking, of the compilation of catalogs or area lists with intent of producing further area studies. Such listings include Colorado (Shushan & Anderson, 1969), Mexico (Imshaug, 1956), New Mexico (Egan, 1972), Long Island, New York (Brodo, 1968), Wyoming and South Dakota (Wetmore, 1967), and Washington (Thomson, 1969). Our Canadian colleagues have produced similar inventories on Quebec (Lepage, 1947-1949, 1958); Alberta, Saskatchewan, and Manitoba (Bird, 1966); British Columbia (Ahti & Otto, 1967); and Yukon (Bird, 1967). Wetmore has compiled one on Tasmania (1963) and Imshaug one on the West Indies (1957). Nor should we forget the extremely helpful checklists of North American lichens compiled by Hale and Culberson (1956, 1960, 1966, and 1970).

Extraterritorial papers have been produced on South America, the Galapagos Islands, Antarctica, and the Antarctic Islands by G. A. Llano, W. A. Weber, I. M. Lamb, C. W. Dodge, and E. D. Rudolph. These very numerous and intensive papers are not listed here but can easily be found in the Culberson literature listings. They represent a very large step forward, especially in the most important vegetation of Antarctica, an area which has but two angiosperms, 50 mosses, and over 400 species of lichens.

MANUALS AND AIDS

Perhaps most important in the recruitment of new talent and interest in lichenology is the production of manuals and illustrated books for the beginner. The *Lichen Handbook* (1961) and *How to Know the Lichens* (1969) by Mason E. Hale, Jr. are among the most important advances in our field, as they open the field to beginners. Hitherto it was very difficult to get a start in lichenology without the assistance of someone to guide the first steps in identification. These new manuals, containing illustrations and keys, of the common larger species of foliose and fruticose lichens make it possible for a beginner to get a reasonable start in lichenology. The crustose lichens are still a difficult task, and although outdated the Fink *Lichen Flora* (1935) is still the only reference for a starter to use. Very fine manuals for the beginner to use are the Taylor *Lichens of Ohio*, parts 1 and 2 (1967, 1968), covering the larger lichens of that state. For the beginner in lichen chemistry the appropriate parts of Hale (1961), Taylor (1967,

1968), or Thomson (1967c) will serve well in securing a foundation knowledge as they are well illustrated with the crystalline reaction products. For continued study, *The Bryologist*, published by the American Bryological and Lichenological Society, is essential as it has many articles on lichens in its issues. As an entrance into the literature it is also essential to consult the series of listings "Recent Literature on Lichens" which William Culberson founded in 1955 while at the University of Wisconsin and which he still produces for practically every issue of *The Bryologist*. It is a very essential service because the literature of lichenology is so far scattered amid so many and sometimes obscure publications. In this connection it is necessary to note the founding of the British Lichen Society in 1958 and its publication *The Lichenologist* with a first number in 1958 and a continual enlargement and improved quality since then. The British Lichen Society boasts of over 400 members, attesting to the swelling interest in these organisms (?). Even more recent is the founding of the *Lichenological Newsletter* in April 1967 by Vernon Ahmadjian, Irwin Brodo, and Mason E. Hale, Jr., as a "house organ" by which lichenists can keep informed of each other's activities and opinions. The typesetting and printing of this is done by Hale and son as a labor of love. An International Association for Lichenology was also formed during the XI Botanical Congress at Seattle. Vernon Ahmadjian (United States) and Irwin Brodo (Canada) serve as the American representatives on the council.

LICHEN ECOLOGY

Turning now to ecological studies of lichens, we find several new and important aspects of lichenology have developed in this continent over the past quarter century. Earlier works of ecological nature had been produced by Bruce Fink and his students. In the main, these consisted of lists of lichens growing in particular habitats. A break with this tradition occurred in a paper by Wolfe, Wareham, and Scofield (1949) emphasizing the influence of microclimates on plant distributions. A major new approach to the ecology of cryptogams is exemplified by the papers of Hale (1952a, 1955) and W. L. Culberson (1955a, 1955b), who utilized the ordination of communities and their components, mosses and lichens, to obtain an unbiased reflection of the situation in the field in the forests of Wisconsin. Studies using similar approaches but enlarging the scope of the communities have been published by Looman (1964) on grasslands and by Foote (1966) on rock outcrops. Deeper incursion into the mathematics of such ecologies may be found in the works of Beals (1965) and Yarranton (1969).

For some reason, perhaps the slowness of growth rates in lichens, there seems to have been a strong interest in measurement of this, and a number of papers have appeared on this subject, notable ones being by Hale (1954, 1959), Brodo (1965), Pegau (1968), and Scotter (1963). An important application of studies on growth rate became known as lichenometry through the perspicuous and internationally famous work of the late Roland Beschel of Canada. Beschel made numerous studies of the retreats of glaciers and icecaps, using the age of lichens as a dating device (Beschel, 1961). The oldest lichens known to him, according to his publications, were 4,500 years of age, among the world's oldest

living things. The productivity of lichens has barely been touched with one paper on alpine lichen productivity by Bliss (1966) and one by Scotter (1962).

With the advent of the nuclear bombs and the worldwide dissemination of the products of the tests, there came an interest in the fallout of the tests and their influence on the lichens, which obtain a large part of their mineral nutrition from the dusts of the atmosphere. The classic paper in this field is that by Palmer *et al.* (1963) on cesium-137 in Alaskan Eskimos, pointing out the short food chain involving only lichens, caribou, and Eskimos of the Anaktuvuk Pass, Alaska, region. This short chain brings unusually high radioactivities to man. A further paper by Salo and Miettinen (1964) showed the accumulation of strontium-90 and cesium-137 in arctic vegetation, and still further papers by Hanson (1967) and Plummer and Helseth (1965) have also dealt with this problem. A paper by Woodwell and Gannutz (1967) is important in demonstrating the effects of gamma radiation on a forest lichen community in an experimental setting. Undoubtedly, further researchers will have very much more to say upon this extremely serious problem.

Another environmental problem, although not perhaps a new one, since Nylander in the 1850's complained of the influence of the air pollution in Paris on lichen distributions, is that of air pollution. Studies of the relationships of lichens to polluted air have been common for some time in Europe. In fact, certain lichens, according to Barkman, have become extinct in parts of Europe as a consequence of air pollution. LeBlanc and Rao, in Quebec, have made such problems a major study and a classic paper is theirs on the effects of the pollution by an iron-scinterring plant in Ontario on the cryptogamic vegetation (Rao & LeBlanc, 1967). In other studies they have published on the effects of urban environments on lichen distributions (LeBlanc, 1961). Another important paper is that by Brodo (1966) on lichen ecology in central Long Island, New York, pointing out the effects of air pollution in that region.

A paper in lichen ecology important in introducing a new technique for transplanting corticolous lichens (or mosses) by the use of bark plugs is that by Brodo (1961*b*).

Comparatively few studies of water and temperature relations of lichens have been carried out in this country. These have been the subject of investigations in Germany and Japan especially. But a few investigators on this continent should be mentioned, including L. C. Pearson (1969), who studied the influence of temperature and humidity on the distribution of lichens in a Minnesota bog, and Klepper (1968), who compared the water relations of a moss and a lichen.

The first of papers involving the physiological ecology of lichens has just appeared from the laboratory of Michael Adams (1971), but the future will see a number of studies in this genre as his students come to the publishing stage. Currently he is working on the rates of photosynthesis and respiration as influenced by external factors.

William Weber (1962, 1967) has written on environmental modification in crustose lichens in the arid Southwest, showing that some of the modifications which have been called species are merely the same plant under different environ-

mental conditions. These are important papers, expressing a point of view shared by many lichenologists.

The relationships between caribou, forest fires, and lichens have been reported upon in depth by G. W. Scotter in a series of papers (1962, 1963, 1964, 1967).

Much work remains to be done in lichen ecology. Only a few of the communities have been adequately described and little is known of the autecology of any of the species. Looking ahead shows this a field with much promise for studies.

LICHEN PHYSIOLOGY

The physiology of the lichen combination and of its components is under very active investigation in Europe, particularly in Britain and Holland, as well as Germany and Finland. In North America this field is mainly developed by Vernon Ahmadjian and his students. After a long series of experiments with the isolation of lichen components and their resynthesis into lichens, he has achieved the greatest success with *Endocarpon pusillum* and *Staurothele clopima* (Ahmadjian & Heikkila, 1970). A very fine summary of this area of investigation, one which seems to challenge lichen physiologists most, is contained in the book *The Lichen Symbiosis* by Ahmadjian (1967). This book is important also in suggesting intriguing problems for further investigation. L. C. Bliss has been contributing studies on photosynthesis and respiration in alpine lichens (Bliss & Hadley, 1964). As already mentioned, Michael Adams is pursuing a similar field of endeavor, and we can look forward to contributions from such investigations. It would seem to me that the area of lichen physiology is currently under exploited in this country and that there is a good possibility for further contributions.

MORPHOLOGY

The current status of studies of lichen morphology is that it is surprisingly quiescent on this continent. Excellent contributions are coming from Britain, Germany, France, and Scandinavia, but little from North America. Two papers influential in directing thought on a problem of importance in taxonomy as well as morphology are Weber's (1962, 1967) papers on the influence of the environment on the structure of crustose lichens. By influencing the characteristics of the lichens, the environment has brought about modifications which some taxonomists have translated into superfluous species. A major interest in morphology in North America seems to be the use of the new tool, the electron microscope, in studying the ultrastructure of lichens. As yet, only a few contributions have appeared: a general survey by Jacobs and Ahmadjian (1969), one on *Xanthoria* by Bednar and Juniper (1964), one on *Physcia aipolia* by Rudolph and Giesy (1966), and another on the same lichen by Brown and Wilson (1968), and one on *Endocarpon pusillum* by Ahmadjian and Jacobs (1970) are samples of the state and development of the art. I have seen only one paper on lichens using the still more recent instrument, the scanning electron microscope, by Hawksworth (1969) of England on the surface of various *Alectoria* species, demonstrating that this tool indeed may be of help in lichen studies.

ECONOMIC USES

Little investigation on economic uses of lichens has been made. Two review articles by G. A. Llano (1948, 1951) constitute the major contribution in this area and are mainly concerned with historical uses, although also giving an excellent description of current practices using lichens in home-dyeing in Sweden. A book by Eileen Bolton (1960) makes available to the layman the results of her experiments in the use of lichens as dyestuffs. An earlier period of investigation of lichens as sources of antibiotics seems to have run its course, and no further papers have appeared upon this topic in recent years.

In summary, it may be stated that the currently strong fields in the investigation of lichens include chemistry, and also its relationship to taxonomy; taxonomy, with immense amounts yet to be done; distributions over the continent which need to be studied, with that of many states comparatively unknown, and the lichens of Mexico which are especially in need of study. Ecological studies are in progress at a number of institutions, and many opportunities still exist in this field for investigation. Lichen physiology is under investigation but with much yet to be learned. Morphology and economic uses are currently of scant interest and yet could be revived in the future. The interest in lichens as subjects of investigation should continue the strong and steady increase which has been shown in the last quarter century.

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